Running head: North American *Bacidia fuscoviridis*

# *Bacidia fuscoviridis*, another overlooked sorediate crustose lichen widely distributed in temperate eastern North America

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**Abstract.** *Bilimbia fuscoviridis* (≡ *Bacidia fuscoviridis*) is newly reported from North America where it is shown to be widespread in the temperate eastern United States and adjacent Canada, frequently occurring on shaded calcareous rocks and siliceous rocks in humid habitats near waterways. A detailed description based on North American material is provided, the distribution is mapped, and color photographs are provided. The species is likely common but overlooked due to its inconspicuous appearance and the absence of diagnostic secondary metabolites.

**Key words.** Asexual reproduction, biodiversity, floristics, limestone, soredia, sterile sorediate crust.

## Acknowledgements

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Taxonomic and floristic research on lichens in North America has long focused on foliose and fruticose macrolichens, and taxa that routinely form sexual fruiting bodies (Hodkinson and Lendemer 2012; Lendemer and Coyle 2022). This reflects the ease of collection and detection for macrolichens, the emphasis on sexual characters in taxonomic frameworks, and the perception that asexually reproducing lichens are both difficult to identify and evolutionary dead ends (Poelt 1970; Bergamini *et al.* 2005, 2007; Tripp 2016; Lücking *et al.* 2021; Lendemer and Coyle 2022). Yet, in most North American systems, macrolichens are less species rich than crustose microlichens, and taxa with dominant asexual reproductive modes represent a more substantial component of biological diversity than has previously been believed (e.g., Lendemer *et al.* 2016a; Lendemer 2018; Tripp *et al.* 2019, 2022; Waters and Lendemer 2019). The intersectionality of crustose microlichens with dominant asexual reproductive modes has resulted in major knowledge gaps for a group of ecologically important and species rich fungal mutualisms (Hodkinson and Lendemer 2012; Allen & Lendemer 2022).

Temperate eastern North America hosts the highest diversity of lichens on the continent, including many microlichens with dominant asexual reproductive modes (Tripp *et al.* 2022). Intensive studies during the last two decades have substantially improved understanding of the diversity and distributions of these organisms (e.g., Lendemer 2013). This is especially the case for taxa that are frequent and abundant across a wide spectrum of habitats, and many of which were only recently reported or described (e.g., Lendemer 2011; Lendemer *et al.* 2016b; Muscavitch *et al.* 2017). Nonetheless, despite such focused attention, new and previously overlooked taxa continue to be found (e.g., McMullin *et al.* 2020; Lendemer and Keepers 2021; Curtis and Lendemer 2022).

For nearly two decades, the last author has collected a distinctive sorediate crustose lichen at scattered locations throughout eastern North America. It is unusual in lacking secondary metabolites, having minute soralia with bright yellow-green soredia, a conspicuous white prothallus, and in often occurring on calcareous rocks or rocks along waterways (Harris and Lendemer 2005; Lendemer 2005; Waters and Lendemer 2019; Waters 2022; Fig. 1 herein). Despite having seen over a dozen collections from locations across much of temperate eastern North America, and the combination of distinctive characters, the species remained unconnected to an existing name. Recently the first author collected a fertile specimen of the species, and a renewed effort to compare it with other taxa described in the literature led to the recognition that it was *Bacidia fuscoviridis*, a species widespread in Europe but as yet unreported from North America (Esslinger 2021). Here we report on the discovery of *B. fuscoviridis* in North America, provide a detailed description of the North American material, summarize its known geographic distribution and ecology, and provide color photographs of the species to aid in the documentation of additional occurrences. We also present new analyses of existing DNA reference sequences that support prior assertions that *Bacidia fuscoviridis* does not belong to *Bacidia* De. Not. s.str. Based on our results we suggest it should instead be returned to *Bilimbia* De. Not. where it was originally described nearly two centuries ago.

## Methods

This study is based on specimens deposited in the R. L. McGregor Herbarium at University of Kansas (KANU), Tom S. and Miwako K. Cooperrider Herbarium at Kent State University (KE) and the New York Botanical Garden (NY). Specimens at KE were examined dry using a Fisher Scientific Stereomaster dissecting microscope. Specimens at KANU and NY were examined dry with an Olympus SZ-STB dissecting microscope and mounted sections were examined with an Olympus BX53 compound microscope. Lichen substances were studied using standard spot tests (K, C, KC, P) following Brodo *et al.* (2001). Selected specimens were also studied with Thin Layer Chromatography (TLC) following Culberson and Kristinsson (1970) as modified by Lendemer (2011) using Solvent C.

To evaluate the generic relationships of *Bacidia fuscovirdis* within Ramalinaceae we carried out BLASTn searches of the existing reference sequences of *B. fuscoviridis* in NCBI which recovered representatives of *Biatora* Ach., *Lecania* A.Massal. and *Mycobilimbia* Rhem, as the closest hits for ITS and the lone sequence of rpb2. Based on these results we used the published phylogeny of Ramalinaceae from Kistenich et al. (2018) as a guide and constructed a multi-locus dataset that mirrored their sampling of the clade containing *Bilimbia*, *Lecania* and *Mycobilimbia* with *Biatora* as an outgroup. We downloaded the mtSSU, ITS, nucLSU and RPB2 sequences used by those authors (see Table 1) and manually aligned each dataset in Mesquite 3.31 (Maddison & Maddison 2017. We then added the available reference sequences of *B. fuscoviridis* (three ITS sequences, one rpb2 sequence) to the relevant alignment, manually adjusted them, and defined all ambiguously aligned regions and gap-rich terminal regions in an exclusion set. The excluded regions were then manually deleted, terminal gaps transformed to missing data, and uncertainties and polymorphisms transformed to missing data. The alignments were then concatenated in Mesquite and exported a single PHYLIP file. The concatenated alignment was partitioned and RAxML v8.2x (Stamatakis 2006) was used to infer a maximum likelihood (ML) topology and bootstrapping was performed with 500 pseudoreplicates and implementing the model GTRGAMMA across all partitions. The results were visualized in FigTree 1.4.3 (Rambaut 2016). Data underlying the molecular phylogenetic analyses presented have been archived at Zenodo as DOI: 10.5281/zenodo.7573693.

## Taxonomic Section

***Bilimbia fuscoviridis*** Anzi, Comment. Soc. Crittog. Ital. 2: 16. 1864. ≡ *Bacidia fuscoviridis* (Anzi) Lettau, Hedwigia 52: 132. 1912. ≡ *Lecidea cupreorosella* var. *fuscoviridis* (Anzi) Stizenb., Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 34(no. 2): 10, tab. I, fig. B, 17-22. 1867. ≡ *Lecidea fuscoviridis* (Anzi) Nyl., Flora, Regensburg 64: 456. 1881. ≡ *Coppinsidea fuscoviridis* (Anzi) S.Y. Kondr., Farkas & Lőkös, in Kondratyuk, Lőkös, Farkas, Jang, Liu, Halda, Persson, Hansson, Kärnefelt, Thell & Hur, Acta Bot. Hung. 61: 301. 2019. TYPE: **ITALY.** [Verbano-Cusio-Ossola Prov.], "ad murum micaceum, vetustum, umbrosum, sine cemento, secus viam, quae ab oppido Suna ducit ad ejusdem oppidi Castellum, supra Lacum Verbanum", *M. Anzi s.n. = Lichenes rariores Langobardi exsiccati No. 403* (TO0022030[digital image!], lectotype **designated here** MBT #10011272; isolectotypes, BM barcode BM001107935 [digital image!], G barcode G00295147 [digital image!], G barcode G00295148 [digital image!], G barcode G00295149 [digital image!], S [digital image!], TO0022147 [digital image!], TO0022701 [digital image!], TO0022702 [digital image!], TO0022813 [digital image!]).

Figures 1 and 2.

TYPIFICATION. – The name *Bilimbia fuscoviridis* does not appear to have previously been typified. The protologue (Anzi 1864: 16) cites "L. Lang. exs. no. 403" as the original place of publication of the name, and hence links it to the specimen distributed by Anzi as number 403 of his *Lichenes rariores Langobardi exsiccati*. Anzi (1864: 17) also gave the provenance of his material as "Sopra un vecchio di micaschisto, senza cemento, tra il borgo di *Suna* e il Castello (Lago Maggiore)". The label distributed with number 403 indicates the material was from "ad murum micaceum, vetustum, umbrosum, sine cemento, secus viam, quae ad oppido *Suna* ducit ad ejusdem oppidi Castellum, supra Lacum Verbanum". The city of Suna was merged into Verbania and is located in the province of Verbano-Cusio-Ossola in the Piedmont region of Italy.

Anzi's herbarium is deposited in TO (Stafleu and Cowan 1976: 55) and hence it would be logical to select a lectotype from the material at that institution. We examined digital images of *Lichenes rariores Langobardi exsiccati* number 403 from multiple herbaria and confirmed that they represent *B. fuscoviridis*. We also contracted TO, whose curators generously sent images of the relevant material from Anzi's herbarium. After discussion and input from S. Favero Longo at TO, we select what appears to be the best specimen from Anzi's herbarium as the lectotype, which includes multiple apothecia that do not appear to be discolored.

DESCRIPTION. – Thallus thin to moderately thick, saxicolous, tightly adhered to substrate, varying from pale green to dark green or olive, often accumulating silt and algae which can obscure the thallus, initially smooth but soon becoming rimose-areolate in maturity, forming either a thin continuous layer or areas of thin, scattered, and slightly elevated areoles at younger portions of thallus, up to 425 µm thick; hypothallus absent or present, often forming a pale outline, sometimes becoming fibrous; areoles irregular, more prominent and sometimes even forming blastidia in older portions of thallus; medulla typically forming an apparent, white layer below the cortex and photobiont in mature portions of thallus, comprised of hyaline hyphae, up to 100 µm thick; cortex mostly present, hyaline, up to 65 µm thick; soralia initially small and punctate, comprised of 3–5 soredia, soon becoming diffuse or forming a linear or maze-like pattern, often corresponding to cracks in the thallus, typically a pale lime-green color contrasting with the darker thallus; soredia small, spherical to irregularly rounded in shape, ecorticate, (17)–31–(52) µm in diameter; apothecia rare, biatorine, 0.2–0.4 mm in diameter, plane to convex, dark brown or reddish-brown, with a well-developed margin that becomes excluded with age;

epihymenium, variably pigmented, hyaline but often with extensive patches of brown pigment that reacts K-; hymenium hyaline, not inspersed, 50-80 µm tall; hypothecium hyaline to pale yellowish-brown, 60–100 µm thick in center; exciple well-developed, 80-130 µm wide, prosoplectenchymatous, composed of thick, densely packed hyphae, hyaline internally and with a layer of brown pigment extending from the epihymenium onto the outermost layer of cells, often with a patch of blue-green pigment that reacts K- and is located on the inner exciple adjacent to the hymenium; paraphyses simple, with the apical cell slightly swollen; asci *Bacidia*-type; ascospores hyaline, 8 per ascus, obtuse-ellipsoid to elongate ellipsoid, 0–1–(3) septate, 11.5–17.0 × 3.0–5.3 µm. Pycnidia not seen. Photobiont Trebouxioid, composed of green coccoid cells 7–13 µm in diameter.

CHEMISTRY. – No substances detected by TLC. Thallus K-, C-, KC-, P-, UV-.

DISTRIBUTION AND ECOLOGY. – To date, *Bilimbia fuscoviridis* has been reported from many areas of Europe where it appears to be widely distributed (Czech Republic, Vondrák *et al.* 2007; Germany, Wirth *et al.* 2013; Great Britain and Ireland, Cannon *et al.* 2021a; Hungary, Vondrák *et al.* 2009; Luxembourg, van den Boom *et al.* 1994; Poland, Czarnota 2017; Slovakia, Guttová and Palice 2001; throughout the Alps, Nimis *et al.* 2018). Most reports are from shaded calcareous rocks (e.g., Vondrák *et al.* 2007, 2009) although it has also been reported from basic siliceous rocks (Nimis *et al.* 2018) and siliceous rocks along waterways (Cannon *et al.* 2021a). Occurrences on natural outcrops associated with humid or sheltered microhabitats are often mentioned in the literature (e.g., Nimis *et al.* 2018), however the species has also been reported from rock walls and gravestones (Cannon *et al.* 2021a).

Despite having been collected in the eastern United States for several decades, it was only the discovery of a fertile collection (*T.J. Curtis s.n.*, KE L5445!) that led us to connect the taxon with *Bacidia* De Not., and subsequently to *Bilimbia fuscoviridis* in the literature. Based on the material we have seen, the ecology of the species in North America is very similar to that in Europe. *Bilimbia fuscoviridis* typically occurs on calcareous rocks such as limestone, weakly calcareous or basic shale, and cation rich substrates such as diabase. Most of the known occurrences in North America are from natural rock outcrops in humid and shaded habitats, albeit across a wide selection of different temperate eastern North American forest types dominated by varying degrees of hardwoods and conifers (see Braun 1950). In the Appalachian Mountains, Ozarks and Great Lakes Regions, the species often occurs on rock outcrops directly adjacent to, or within riparian corridors, including areas where it would experience occasional inundation by high water levels (Fig. 3). While in some areas, such as the eastern Great Plains of Kansas, it occurs on massive, north-facing outcrops and cliffs in upland habitats. One occurrence was found on schistose rocks of an old retaining wall (*Lendemer 4432 & Schuyler*, NY!).

The records of *Bilimbia fuscoviridis* seen for this study suggest that the species is widely distributed in temperate eastern North America, with a typical Appalachian-Great Lakes distribution (see e.g., Brodo *et al.* 2001) extending from Ontario, Canada south to Alabama, U.S.A and then westward into the Ozarks and eastern Great Plains (Fig 4). The scattered records reported here almost certainly reflect collector bias against sterile sorediate crustose lichens, especially those that are difficult to collect from smooth, hard rock substrates. We strongly suspect that targeted search efforts will lead to the discovery of additional occurrences throughout the region and that the species is a frequent member of riparian rock lichen communities, and calcareous rock lichen communities.

GENERIC PLACEMENT. – It has been suggested that *Bacidia fuscoviridis* does not belong to *Bacidia* s.str. (e.g., Cannon et al. 2021a), as was explicitly discussed by Reese Naesborg et al. (2007) who included it in a multi-locus phylogeny of *Lecania*. However the species was not included in recent molecular phylogenetic studies of generic delimitation within the broader Ramalinaceae (e.g., Kistenich et al. 2018). It was included in the phylogenetic studies of Ramalinaceae by Kondratyuk et al. (2019) and transferred to the genus *Coppinsidea* S.Y.Kondr., E.Farkas & L.Lőkös., but much of the underlying data for that study remains unpublished and the analyses were not fully described. Our analyses of the existing sequence data for *B. fuscoviridis* in GenBank recovered sequences from three separate European vouchers in a strongly supported (ML: 100) clade that was weakly supported (ML: 65) as sister to *Bilimbia* as represented by *Bilimbia lobulata* (Sommerf.) Hafellner & Coppins and *Bilimbia sabuletorum* (Schreb.) Arnold (Figure 5). The combined clade of *Bilimbia*+*Bacidia fuscoviridis* was in turn recovered in a poorly supported (ML: 33) sister relationship with sequences of *Lecania*, which itself formed a weakly supported clade (ML: 65). The topology recovered in our analyses was congruent with that of Kitsenich et al. (2018) and differed primarily in lower support values within the set of clades comprising *Bilimbia, B. fuscoviridis, Catillaria scotinodes* (Nyl.) Coppins, *Lecania, Thamnolecania* (Vain.) Gyeln. These lower values likely reflect the fact that *B. fuscoviridis* was almost entirely represented by ITS sequences, and that portion of our multilocus alignment included many ambiguously aligned regions due to the variability introduced by inclusion of distantly related taxa. These results also appear to be congruent with Reese Naesborg et al. (2007), as well as Kondratyuk et al. (2019), in the latter the relationships between various genus-level clades were also weakly supported. While further study with additional samples and loci is needed to definitively resolve the generic relationships of *B. fuscoviridis*, based on our results we treat it as a member of *Bilimbia* here given that the taxon conclusively does not belong to *Bacidia* s. str., is more closely related to *Bilimbia*, and a combination in that genus not only exists but is also the basionym.

COMAPRISON WITH SIMILAR SPECIES. – Since sorediate crustose lichens typically lack sexual reproductive structures, they are generally perceived as difficult to identify, especially in the field (Hodkinson and Lendemer 2012). In the absence of the sexual reproductive structures that are often required to inform placement within a given genus or family, species must instead be identified outside the context of a higher-level taxonomic framework by unique combinations of vegetative morphological characters, chemistry, and ecology. While identification is possible when comprehensive taxonomic treatments or floras are available (e.g., Tønsberg 1992), most regions lack such resources for crustose lichens with dominantly asexual reproductive modes. Moreover, new and previously overlooked species continue to be documented and described even in such well-studied areas (e.g., Czarnota and Guzow-Krzemińska 2018; Malíček *et al.* 2018, 2020; Launis *et al.* 2019; Ertz *et al.* 2020). The result is that while a given taxon may be commonly encountered and easily recognized even in the field, it is often difficult to locate a name for the species unless one is already familiar with it in advance (e.g., Harris and Lendemer 2010; Lendemer 2011).

This was the case for the subject of this contribution: *Bilimbia fuscoviridis*. Although not formally reported from North America, this species has previously been referred to as an unidentified sterile sorediate crustose lichen in several checklists published over the last two decades (Harris and Lendemer 2005; Lendemer 2005; Waters and Lendemer 2019; Waters 2022). For several decades it has been collected, often repeatedly, by multiple individuals across its range in eastern North America, all of whom were unable to connect it to the name *B. fuscoviridis*, a species long known from Europe. It was only when fertile material was found that the connection to *Bacidia* and other members of Ramalinaceae or Bacidiaceae was made.

Among the saxicolous sorediate crustose lichens known from eastern North America, there are relatively few that are likely to be mistaken for *Bilimbia fuscoviridis* due to the combination of saxicolous habit, lack of secondary metabolites and bright green or yellow-green soredia that usually contrast strikingly with the thallus (Fig. 1A–D). When *B. fuscoviridis* occurs on calcareous rocks such as limestone and dolomite it is even less likely to be confused with any other species because there are so few sorediate crustose lichens that grow on those substrates in eastern North America. The most similar would be *Acarospora moenium* (Vain.) Räsänen and *Verrucaria furfuracea* (B. de Lesd.) Breuss, both of which are uncommon in the region and generally occur on anthropogenic substrates such as concrete, rather than directly on natural rock outcrops (Weber 1996; LaGreca and Lumbsch 2001; Breuss 2007; Advaita *et al.* 2016). *Acarospora moenium* differs in having dispersed, strongly white pruinose, convex areoles and darkened, black or brown soredia that form in marginal soralia which erode and give the areoles a puffed and crescent appearance (LaGreca and Lumbsch 2001). *Verrucaria furfuracea* differs in having a thallus composed of dispersed to somewhat contiguous brown areoles with marginal, dark brown, short and granular isidia (Breuss 2007). The only persistently sterile crustose lichen that regularly occurs on calcareous substrates in eastern North America and has a somewhat similar thallus color is *Botryolepraria lesdainii* (Hue) Canals *et al.*, but that species is readily distinguished by its thick, leprose thallus and occurrence in sheltered or protected overhangs (Hopkins and Tønsberg 2006; Lendemer 2007).

When *Bilimbia fuscoviridis* is fertile (Figs. 1E and 4, Fig. 2), it is possible that it could be confused with two common, esorediate species that have lecideine or biatorine apothecia and also grow on calcareous rock. *Bacidia granosa* (Tuck.) Zahlbr., is very common in eastern North America and often occurs with *B. fuscoviridis* on calcareous rock outcrops, but it has dark, almost black biatorine apothecia with a dark pigmented hypothecium and exciple, and more consistently 4-celled ascospores (Harris and Ladd 2005; note that Ekman 2014 illustrated and described *B. granosa* as having a weakly pigmented hypothecium). *Lecania cuprea* (A. Massal.) van den Boom & Coppins has biatorine apothecial with reddish-brown apothecial discs and margins that are often darker brown in color and a pale hypothecium (Ekman 2004). Again, although common and widely distributed, neither of these species is likely to be confused with *B. fuscoviridis* unless an abundantly fertile individual with disproportionately few soralia were to be encountered.

*Bilimbia fuscoviridis* is most likely to be confused with other species when it occurs on cation rich substrates such as diabase, and on buffered rock outcrops or boulders in riparian corridors. *Herteliana schuyleriana* Lendemer is a particularly common species of such substrates in shaded temperate forests of eastern North America (Lendemer 2016). While the thallus in that species is continuous, it is thicker, distinctly emerald or blue-green in color, forms coarse blastidia along the cracks and on the surface, and produces atranorin and roccellic acid (Lendemer 2016). *Catillaria patteana* D.P. Waters & Lendemer is a very rare species that is similar in morphology to *B. fuscoviridis*, also lacks secondary metabolites and occurs on cation rich substrates in eastern North America (Waters and Lendemer 2019). That species grows on shaded rocks that are not directly associated with riparian areas, lacks the conspicuous white prothallus that is typically present in *B. fuscoviridis*, and while the soredia are lighter in color than the thallus, they are blue-gray or brownish rather than vibrant green or yellow-green (Waters and Lendemer 2019). In the few collections that are known, *C. patteana* is also often fertile, and in such cases can be separated from *B. fuscoviridis* by the *Catillaria*-type asci and paraphyses with conspicuously swollen apical cells and brown caps (Waters andLendemer 2019).

Although *Lecania croatica* (Zahlbr.) Kotlov is primarily a corticolous species, occasionally it will also grow on non-calcareous rocks in shaded forests. In such cases that species can be separated from *B. fuscoviridis* by its dispersed to somewhat aggregated thallus composed of flattened areoles with marginal soralia (Lendemer and Harris 2010). Anomalous saxicolous occurrences of other sorediate Ramalinaceae or Bacidiaceae, such as *Biatora pontica* Printzen & Tønsberg and *B. printzenii* Tønsberg could also cause confusion, especially the former species which is similar in color to the soredia of *B. fuscoviridis* (Printzen and Tønsberg 2003). Nonetheless both species differ chemically as *B. pontica* produces xanthones and has a C+ orange thallus, while *B. printzenii* produces gyrophoric acid and argopsin and has a C+ pink thallus (Tønsberg 2002; Printzen and Tønsberg 2003). *Bacidia sorediata* Lendemer & R.C. Harris is an additional sorediate species that somewhat resembles *B. fuscoviridis* in color and overall aspect, although the soralia are much larger and diffuse, it produces atranorin, and it is not known to occur on rocks (Lendemer et al. 2016b).

*Ropalospora viridis* (Tønsberg) Tønsberg, is another typically corticolous species that rarely grows on rocks and then can resemble *B. fuscoviridis*, but the soralia are erumpent in that species and it differs chemically in the production of perlatolic acid, so has a UV+ blue-white thallus (Tønsberg 1992; Lendemer 2011). Some sterile, saxicolous thalli of *Bacidina* species (e.g., *B. delicata* (Larbal. ex Leight.) V. Wirth & Vězda) or *Fellhanera* species (e.g., *Fellhanera granulosa* R.C. Harris & Lendemer, *F. hybrida* R.C. Harris & Lendemer, *F. minnisinkorum* R.C. Harris & Lendemer) could be mistaken for *B. fuscoviridis*, and indeed these all lack secondary metabolites (Harris and Lendemer 2009). But those taxa differ in the production of goniocysts or blastidia rather than the punctate to irregularly elongate soralia of *B. fuscoviridis* (Ekman 1998; Harris and Lendemer 2009b). Due to their intense green coloration and thalli formed of minute goniocysts, members of the *Micarea prasina* Fr. group also resemble *B. fuscoviridis* to some degree in the field, although these only rarely grow directly on rock and the thalli are uniform in color as well as frequently fertile (Barton and Lendemer 2014; Launis *et al.* 2019). Members of that group also produce secondary metabolites, particularly methoxymicareic acid or micareic acid, and so they differ chemically from *B. fuscoviridis*, although those substances require TLC to detect and are sometimes present in low concentrations (Barton and Lendemer 2014). *Micarea soralifera* Guzow-Krzem., Czarnota, Łubek & Kukwa is a member of the *M. prasina* group that has a minutely areolate, sorediate thallus and hence there could be greater potential for this species to be confused with *B. fuscoviridis* (Guzow-Krzemińska *et al.* 2016). Like other members of the *M. prasina* group, *M. soralifera* occurs on bark and lignum, and differs from *B. fuscoviridis* chemically in the production of micareic acid (Guzow-Krzemińska *et al.* 2016).

There are several other crustose lichens that occur on non-calcareous rock outcrops in sheltered or protected microhabitats and could be confused with *Bilimbia fuscoviridis* even though they all have *Trentepohlia* Mart. photobionts rather than the green coccoid algae of *B. fuscoviridis* (Lendemer 2009). These species include *Enterographa zonata* (Körb.) Källsten ex Torrente & Egea, *Gyrographa gyrocarpa* (Flotow) Ertz & Tehler, *Opegrapha moroziana* Lendemer, and *Psoronactis dilleniana* (Ach.) Ertz & Tehler. *Enterographa zonata, G. gyrocarpa* and *O. moroziana* have sorediate thalli but can easily be separated from *B. fuscoviridis* by their chemistry (confluentic acid in *E. zonata*, gyrophoric acid in *G. gyrocarpa* and psoromic acid in *O. moroziana*) (Wirth 1970; Kashiwadani and Thor 1995; Lendemer 2009). *Psoronactis dilleniana* is not distinctly sorediate, but instead produces a scurfy thallus that superficially resembles a thick, granular crust and has psoromic acid (Ertz *et al.* 2015; Cannon *et al.* 2021b). When fertile, *P. dilleniana* produces pruinose, black, lecideine apothecia and transversely septate ascospores (Ertz *et al.* 2015; Cannon *et al.* 2021b).

Several other sterile, saxicolous crusts that produce soralia differ most notably in chemistry, such as *Phlyctis petraea* R.C. Harris, Muscavitch, Ladd & Lendemer, *Porpidia degelii* (H. Magn.) Lendemer, *P. soredizodes* (Lamy ex Nyl.) J. R. Laundon, *P. tuberculosa* (Sm.) Hertel & Knoph, and *Trapelia placodioides* Coppins & P. James which all produce secondary metabolites detectable with standard spot test following Brodo *et al.* (2001) as well as thin-layer chromatography (mainly gyrophoric, norstictic, and/or stictic acids) (Nash *et al.* 2004; Lendemer and Harris 2014; Orange 2018; Muscavitch *et al.* 2017) while *B. fuscoviridis* does not. These species also generally differ in thallus color, ranging from brownish to pale gray or white (rarely even immersed) rather than greenish as in *B. fuscoviridis*. *Fuscidea recensa* (Stirton) Hertel, V. Wirth & Vězda, another saxicolous, sorediate crust, is quite common in eastern North

America and shares much sympatry with *B. fuscoviridis* (Fryday 2008; Lendemer 2009a) but differs in its more grayish to brownish color, more acidic or siliceous substrata, and the production of divaricatic acid (Nash *et al.* 2004). It is also often fertile, and its apothecia differ in being lecideine (Fryday 2008) rather than biatorine as in *B. fuscoviridis*. Several species in the family Teloschistaceae, such as *Caloplaca pratensis* Wetmore and *C. reptans* Lendemer & Hodkinson, also form dull, sorediate thalli on rocks that are not always fertile, but the thalli of these species differ in their grayish color (Wetmore 2009; Hodkinson and Lendemer 2012). *Caloplaca reptans* also differs morphologically in being minutely lobate, rather than smooth and rimose as in *B. fuscoviridis*, and occurs more often on non-calcareous rock (Hodkinson and Lendemer 2012).

*Selected Additional Specimens Examined.* **CANADA.** Ontario. Lanark Co., 0-0.2 mi N of Peneshula Rd., 0.6 mi W jct w/ Cedar Cove Rd., 21 May 2011, on limestone, *J.C. Lendemer 28200 & R.E. Lee* (NY). **U.S.A.** Alabama. Cherokee Co., Wolfden Flats, off CR45, NNW of Rock Run, 3 Oct. 1999, on rock, *R.C. Harris 43410* (NY). Arkansas. Benton Co., Hobbs State Conservation Area, along Page Sawmill Rd. 0.35 mi NE of jct w/ Rambo Rd., 16 Oct. 2005, on shaded limestone, *J.C. Lendemer et al. 5340* (NY); Ozark National Forest, Wedington Small Game Area, just S of Illinois River, 12 Apr. 2004, on dolomite, *R.C. Harris 48826* (NY). Kansas. Cherokee Co., NE of SE Bagdad Rd. ~0.2 mi W of Missouri State line ~1.6 mi E of US160/400, 31 Oct. 2000, on limestone, *D. Ladd 22441* (NY). Douglas Co., University of Kansas Campus, 15 May 2013, on limestone gravel, *C.A. Morse 23923d* (KANU); Fitch Natural History Reservation, 20 Dec. 2017, on limestone outcrops, *C.A. Morse 25891* (KANU); ca. 0.5 mi N, 5.6 mi W of Lecompton, along S side of Scenic River Rd. (= N 2190 Rd.), 28 Apr. 2015, on limestone outcrop, *C.A. Morse et al. 24493* (KANU). Jefferson Co., ca. 1 mi S, 3 mi E of Ozawkie, E side of Perry Lake, 11 Oct. 2015, on limestone, *C.A. Morse et al. 24868* (KANU). Johnson Co., Overland Park Arboretum and Botanical Garden, 8 Jun. 2007, on limestone bluff, *C.A. Morse et al. 15323* (KANU). Leavenworth Co., Fort Leavenworth Military Reservation, NW part, 14 May 2008, on shaded sandstone along draw, *C.A. Morse 16458* (KANU). Linn Co., Dingus Natural Area, 11 Oct. 2018, on HCl+ sandstone boulder, *C.A. Morse 26509b & C.C. Freeman* (KANU). Miami Co., North La Cygne State Fishing Lake and Wildlife Area, 11 May 2008, on limestone outcrops, *C.A. Morse 16432 & K. Logan* (KANU). Missouri. Buchanan Co., Bluffwoods Conservation Area, 6 Jun. 2008, on limestone, *C.A. Morse 17363 & D. Ladd* (KANU). Maries Co., Spring Creek Gap Conservation Area, E of CR340, 4 Nov. 2002, on rock, *R.C. Harris 46581* (NY). Perry Co., Seventy-Six Conservation Area, E of MO Hwy. D, 13 Oct. 2003, on limestone, *W.R. Buck 45195* (NY, fertile). New Jersey. Hunterdon Co., Wickecheoke Greenway, ~41 Upper Creek Rd., 28 Apr. 2020, on siliceous rock, *D.P. Waters 4929* (NY); Wickecheoke Greenway, trail near 64 Lower Creek Rd., 10 June 2020, on siliceous rock, *D.P. Waters 5084* (NY). Mercer Co., Mercer Meadows County Park, Stony Brook Corridor, 25 Sept. 2016, on shale, *D.P. Waters 2314* (NY). New York. Clinton Co., Valcour Island, Bluff Point, 18 May 2007, on dolomite, *R.C. Harris 53562* (NY), *R.C. Harris 53564* (NY). Greene Co., Catskill

Mountains, N end of Mink Hollow and E slope of Sugarloaf Mountain, 8 Oct. 2007, on sandstone, *J.C. Lendemer 9743 & A. Moroz* (NY). Ohio. Ashland Co., Mohican State Park, 30 Jun. 2018, on shale rocks, *T.J. Curtis s.n.* (KE L4099). Columbiana Co., Liverpool Twp., Beaver Creek St. Forest, approx. 3,900 ft SE of the Fisher Rd/Calcutta-Smith Ferry Rd jct, 2 Nov. 2019, on sandstone boulder at creek bank, *T.J. Curtis s.n.* (KE L4109, NY); Middleton Twp., Sheepskin Hollow Nature Reserve, approx. 4.5 mi E of Clarkson, 11 Apr. 2020, on moist shale/sandstone of a small outcropping, *T.J. Curtis s.n.* (KE L5445). Cuyahoga Co., Orange Twp., Shiverick property, approx. 1,400 ft W of the Fairmount Blvd/Chagrin River Rd jct, 9 Nov. 2019, on moist granite and shale in stream bed, *T.J. Curtis s.n.* (KE L4200). Geauga Co., potential CMNH property along Kile Rd., 3 Aug. 2018, on shale on a small sandbar, *T.J. Curtis s.n.* (KE L4100). Mahoning Co., Youngstown, Mill Creek Park, 3 Feb. 2018, on a moist sandstone rock face w/ mineral deposit (weakly calcareous?), *T.J. Curtis s.n.* (KE L4097), 3 Nov. 2018, on a moist sandstone rock face w/ mineral deposit (weakly calcareous?), *T.J. Curtis s.n.* (KE L4096). Summit Co., Cuyahoga Falls, Gorge Metro Park, 3 Aug. 2018, on large sandstone boulders in an ephemeral stream bed, *T.J. Curtis s.n.* (KE L4098). Pennsylvania. Bucks Co., Bowman's Hill Wildflower Preserve, 26 Oct. 2017, on hornfels, *D.P. Waters 3079* (NY), 6 Oct. 2017, on shale, *D.P. Waters 3026* (NY); Nockamixon State Park, small tributary to Tohickon Creek, 30 Mar. 2004, on diabase, *J.C. Lendemer 2133 & A.F. Rhoads* (NY); Ralph Stover State Park, SE corner of park, 15 Sept. 2007, on periodically submerged shale, *J.C. Lendemer 9702 & A. Moroz* (NY); Ringing Rocks County Park, 15 Sept. 2005, on boulders, *J.C. Lendemer 4955* (NY). Clinton Co., Logan Twp., St Game Lands 295, approx. 2.9 mi SE of the Rodgers Rd/Narrows Rd jct, 28 Dec. 2019, on a sandstone boulder, near bank of Fishing Creek, *T.J. Curtis s.n.* (KE L4923). Huntingdon Co., NW of PA45, 1 mi SW of village of Franklinville, 21 April 2008, on limestone, *R.C. Harris 54190* (NY), *J.C. Lendemer 11681* (NY). Monroe Co., Delaware Water Gap National Recreation Area, Community Drive wetlands/Hogback Ridge, 24 April. 2004, on rock, *R.C. Harris 49592* (NY), *J.C. Lendemer 2287* (NY), 17 Sept. 2005, on shaded boulder, *J.C. Lendemer 4964* (NY); Delaware Water Gap National Recreation Area, along Freeman Tract Rd./River Rd. North, 25 Apr. 2004, on rock, *J.C. Lendemer 2679* (NY). Philadelphia Co., Wissahickon Park, 24 Jun. 2005, on schistose rock in rock wall, *J.C. Lendemer 4432 & A.E. Schuyler* (NY). Tioga Co., Tioga State Forest, E shore of Gleason Hollow Run at confluence with Fahneystock Run, 14 May 2009, on sandstone in overhang, *J.C. Lendemer 16931* (NY). York Co., York County Bridge No. 6, Mill Creek, W of confluence with Susquehanna River, 27 May 2009, on rock, *J.C. Lendemer 17949* (NY). Tennessee. Blount Co., Great Smoky Mountains National Park, White Oak Sinks, 13 Oct. 2010, on limestone, *J.C. Lendemer et al. 26880* (NY). West Virginia. Pocahontas Co., Monongahela National Forest, S-facing slopes of Gay Knob, 18 Sept. 2022, on sandstone, *J.C. Lendemer 77053* (NY).

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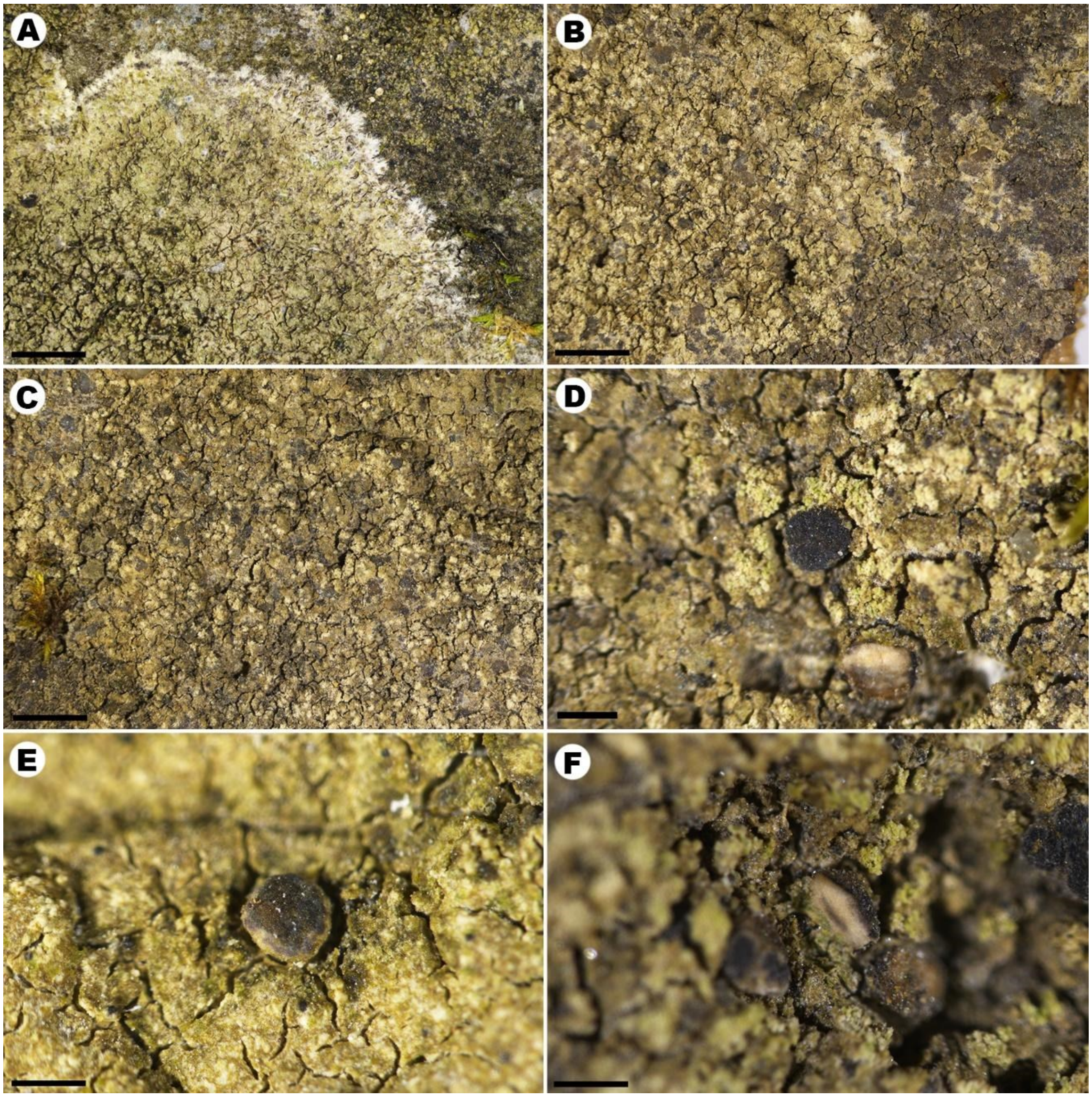

Figure 1, morphology of *Bilimbia fuscoviridis* (A from *Harris 53562*, B-D and F from *Curtis s.n.* at NY, E from *Lendemer 2133*). A, gross morphology of typical thallus with well-developed white prothallus. B, gross morphology of thallus with poorly developed white prothallus. C, typical appearance of small soralia with the naked eye. D, detail of soralia and apothecium. E, detail of apothecium and adjacent minute soralia. F, transverse section of an apothecium. Scales = 2.0 mm in A-C, 0.5 mm in D-F.

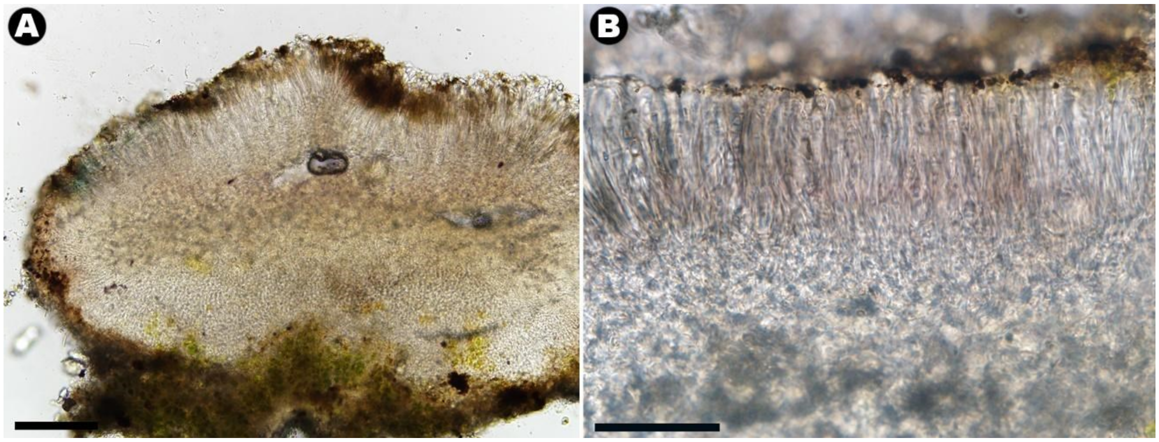

Figure 2, anatomy of *Bilimbia fuscoviridis* apothecium (from *Curtis s.n.*, NY). A, transverse section of apothecium mounted in water. B, hymenium illustrating epihymenial pigmentation and asci.  Scales = 1000 µm in A, 50 µm in B.

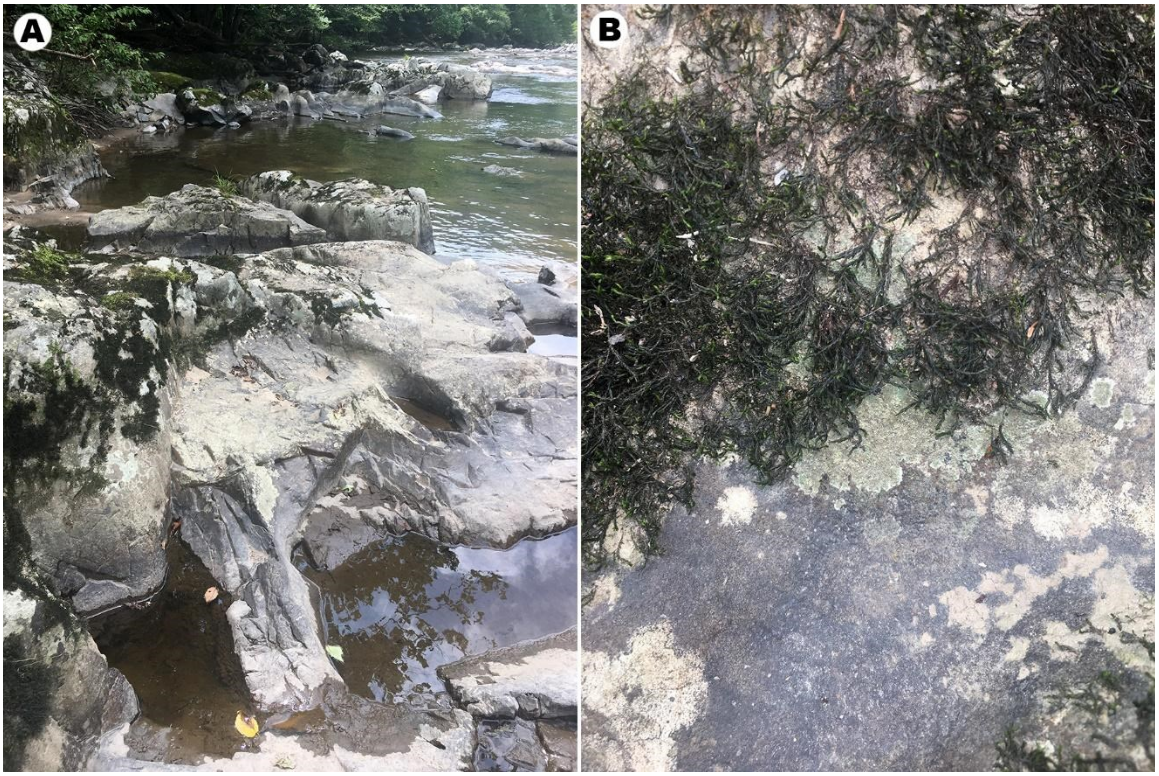

Figure 3, ecology of *Bilimbia fuscoviridis*. A, typical rock outcrop habitat in a riparian corridor (Laurel River near Hot Springs, Pisgah National Forest, North Carolina, U.S.A.). B, thallus of *B. fuscoviridis* partially covered with mosses on periodically submerged rocks.

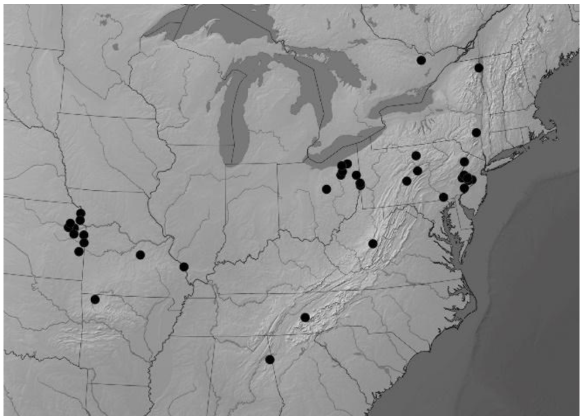

Figure 4. Known geographic distribution of *Bilimbia fuscoviridis* in North America based on specimens examined for this study.

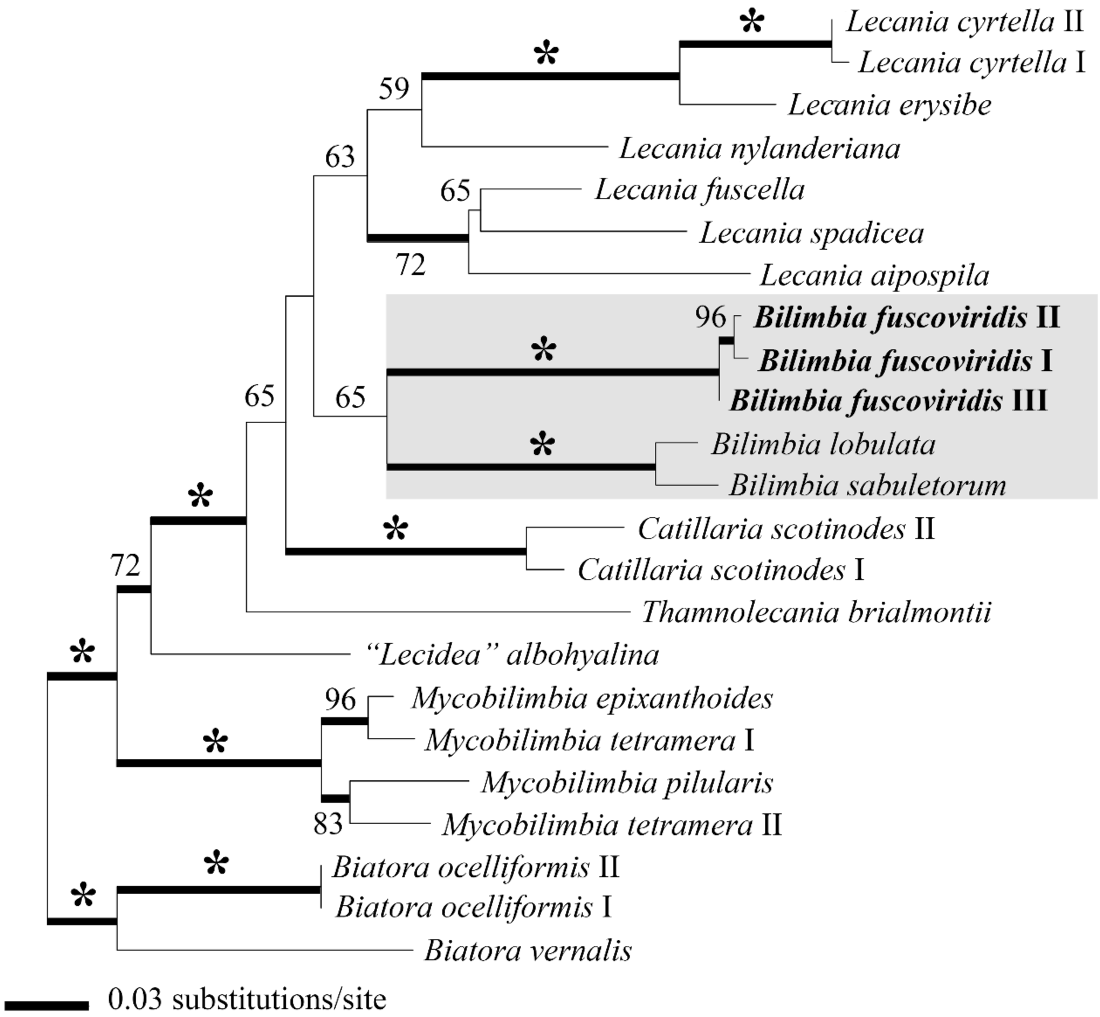

Figure 5. Phylogeny of *Bilimbia* and related genera in Ramalinaceae mirroring sampling by Kistenich et al. (2018), including all reference sequences of *B. fuscoviridis* from GenBank and with *Biatora* selected as outgroup based on the aforementioned publication. Inferred from mtSSU, nucLSU, ITS and rpb2 sequence data and presented as the most likely tree with maximum likelihood bootstrap support values associated with each branch, asterisks "*" representing support of 100, and values >70 treated as supported with corresponding branches thickened. Terminal names correspond to Table 1 and the clade of *Bilimbia*+*B. fuscoviridis* is highlighted in gray.